THE EYES OF THE BLIND VERTEBRATES OF NORTH AMERICA, II. THE EYES OF *TYPHLOMOLGE RATHBUNI* STEJNEGER.*

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WITH PLATES III AND IV.

The caves of North America are inhabited by three salamanders whose eyes range in their structure from the perfectly normal to the most degenerate known among the Batrachia.

Spelerpes maculicauda (Cope) is common in the caves of the Mississippi Valley. As far as I have been able to determine, its eyes have not undergone any degeneration. (Fig. 10.) It is abundant and so nearly allied to *Spelerpes longicauda* Green, an epigean species of very wide distribution, that it has until recently been considered identical with it.

Typhlotriton spelæus Stejneger, is restricted to the western caves of the Mississippi Valley. It has so far been found in Marble Cave and Rockhouse Cave, and smaller caves in the same neighborhood in southwestern Missouri. It is found under rocks in and out of the water. This is the most interesting form inasmuch as it is a much more typical cave animal than *Spelerpes*, but has not yet reached the degenerate condition of *Typhlomolge*. Its eyes are apparently normal in the larva, but in the adult have undergone marked degeneration. (Fig. 11.) The eye-lids are disappearing, and the rods and cones are no longer present in the adult. The eyes of this species will be dealt with in another place.

Typhlomolge rathbuni Stejneger, is found in the underground streams near San Marcos, Texas. It has been secured from the

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artesian well at San Marcos, and from a surface well. It has also been noticed in one of the caves near that place, Ezel's, in which the underground water can be reached. It is said to have come out of some artesian wells south of San Antonio. It is a perennibranch and spends all of its time in the water. Its remarkably long and slender legs are unable to support its body when out of the water. Its eyes form the basis of the present paper. (Fig. 12.)

In February, 1896, the first recorded specimens of this species were cast up from an artesian well about 190 feet deep, bored by the U. S. Fish Commission. Other specimens have since been thrown up at the rate of thirty to fifty a year.

The U. S. Fish Commission, through Dr. B. W. Evermann, sent me four specimens of this salamander and a number of its eggs. The late Prof. W. Norman, of the University of Texas, and Prof. Wm. Bray, of the same place, secured me an additional number. To all of these gentlemen I wish to acknowledge my appreciation and indebtedness.*

The specimens received from the U. S. Fish Commission through Prof. Evermann are as follows:

One adult, received in Washington Apr. 8, 1896.

Three young, of different sizes, received Mar. 11, 1896.

A few eggs laid about Mar. 15, 1896.

The specimens sent me by Prof. Evermann were preserved in alcohol; those sent by Prof. Norman had been killed in Perenyi's fluid. The sections were stained chiefly in Biondi-Ehrlich's tricolor mixture. While the present account contains all that my material warrants me to say concerning these eyes, I appreciate that very much more is left to be done by some one who has access to an unlimited supply of living material of this interesting animal.

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* More recently I visited the caves and artesian well at San Marcos, and have been able to observe the living specimens. On this visit I was put under endless obligations to the very efficient Superintendent of the U. S. Fish Hatchery at San Marcos, Mr. J. L. Leary. My notes on the living salamander, together with Prof. Norman's observations, will be published elsewhere.

The following gives the dimensions of the eyes in a number of individuals. Professor Norman sent only the heads, so I am able to give only approximately the length of those specimens sent by him. The approximate sizes were obtained by comparing the distance between the eyes with the same distance in entire specimens.

		Left Eye		Right Eye	
Length of specimen	Distance between eyes	Longitudinal diameter	Transverse diameter	Longitudinal diameter	Transverse diameter
30 mm.	1.44 mm.	.336 mm.	.232 mm.	.368 mm.	.240 mm.
About 47 mm.	1.92 mm.	.432 mm.	.320 mm.	.432 mm.	.304 mm.
About 70 mm.	3.10 mm.	.544 mm.	.384 mm.	.608 mm.	.368 mm.
.....	.....	.496 mm.	.432 mm.	.544 mm.	.384 mm.
About 90 mm.	4.00 mm.	.592 mm.	.400 mm.	.592 mm.	.448 mm.

The eye of *Typhlotriton* is, in many respects, much more degenerate than that of its European caverniculous relative, *Proteus*. In *Proteus* the six muscles are all present; in *Typhlotriton* they have entirely disappeared. In the former all the layers normal to the retina are present; in the latter the conditions are much simpler. In *Proteus* the lens is still present, and blood-vessels still enter the eye; in *Typhlotriton* no trace of the lens could be found, except in one individual, and blood-vessels no longer enter the eye. While some of the asymmetry may have been caused by reagents, it is evident that there is a great deal of fluctuation in the shape of the eye. The eye is irregular-oval in outline as seen from above, but the optic nerve enters it at the posterior half of its inner face. The eye also increases materially in size from the smallest to the largest of the specimens examined, and this increase is not directly proportional to the increase in the length of the animal, so the young have relatively larger eyes. (Pl. II, fig. 1.)

The eye lies immediately beneath the skin, to which it is attached by a connective tissue mass which is horizontally elongate. The axis of the eye makes an acute angle with the surface of the skin, the eye being directed outward and forward. The dermis over the eye does not differ from that in the neighboring tissues. The epidermis, in the largest individual, is perceptibly thinner over the eye, i. e., from the continuation of

the axis of the eye to the surface of the epidermis. The measurement, in the largest individual, of the epidermis at a point over the eye and 320μ above and below this point gives the following:

Thickness over the eye 73μ, 320μ above the middle of the eye 96μ, 320μ down from the eye 80μ.

The same elements are found over the eye that are evident in other regions. There is no indication of a past free orbital rim; the dermis and epidermis are directly continuous over the eye. There are no eye muscles and no glandular structures connected with the eye. It is surrounded on all sides, except where it becomes associated with the skin, by loose connective tissue meshes, filled with fatty tissue, and is bound to the dermis by many fibres running in various directions, and among these a few pigment cells are found.

SCLERA AND CHOROID.

(a) Largest specimens. Cartilaginous elements are found in the sclera of but two eyes. In one individual 90 mm. long, the left eye possesses a cartilage, while there is none in the right eye. It is in this case placed just above the entrance of the optic nerve, and measures 96μ in thickness, 160μ vertically, and 204μ antero-posteriorly. In all other cases it is a thin, flocculent layer not distinctly separable from the layers beneath it. It is thickest about the entrance of the optic nerve. Over the front of the eye there are a few denser strands which may represent the remains of the cornea. Over the sides of the eye of the largest individual the sclera measures from 4μ to nothing. About the entrance of the optic nerve it attains a thickness of 14μ, and contains here many flat nuclei with a length up to 17μ.

The choroid reaches a thickness of 20μ near the entrance of the optic nerve, and dwindles regularly from this point to the distal face of the eye. Blood-vessels are found in it next to the pigmented epithelium of the eye. Otherwise it is a mass of pigment interlarded with streaks of colorless tissue containing nuclei. Over the front of the eye, next to the epithelium, there are a number of colorless cells with large, granular nuclei.

(b) Essentially the same conditions exist in younger specimens, but the parts are relatively thinner.

The ophthalmic artery, which extends approximately parallel with the optic nerve during its distal course, is sometimes surrounded by pigment. (Figs. 2 and 3.)

THE PIGMENT LAYER, EXCLUSIVE OF THE IRIDEAL PARTS.

The pigment layer is a thin, compact layer, densely pigmented. In an individual 30 mm. long it is about 8μ in thickness. As there are no rods and cones, the inner surface of this layer is similar to the outer, that is, the cells form a pavement epithelium. In places, however, processes of the cells extend in among the cells of the nuclear layers, for a distance of 40μ in some cases (Fig. 2), to the inner reticular layer. In the individuals 70 to 90 mm. long, the pigment epithelium reaches 16μ in thickness.

The only indication of a lens was found in the eye of a specimen 72 mm. long. In this a small lenticular group of cells lay in the opening of the pupil. It measured 24x40μ. (Fig. 9.)

THE IRIS AND ORA SERRATA.

Marked changes take place between the smallest and largest individual examined, so that these must be dealt with seriatim.

(a) The smallest individual 30 mm. long. (Figs. 4 and 5.)

On the left side the pupil measures 22μ in diameter; the distance from the margin of the pupil to the ora serrata measures approximately 100μ. The epithelial portion of this iris consists of an outer layer of dense pigment considerably (14μ) thicker than the pigment epithelium of the rest of the eye. At the pupil this pigment appears rolled into the inner surface of the iris, where it is continuous with the inner layer of cells, which consists of a layer of ordinary pigmentless epithelium 6μ thick, with the nuclei elongate and placed obliquely, and 24μ in length. A few of these ordinarily pigmentless cells show pigment. There is a distinct thickening of the iris at the margin of the pupil. The pigment cells lying on the inner face of this region are much less densely pigmented than those of the

outer layer, and their nuclei are quite evident. The pupil is closed with colorless cells belonging to the choroid. (Fig. 6.)

In the specimen 70 mm. long, very marked changes have been brought about. The pupil was 24μ wide on the right, but is now an oblique channel, and the lower margin of the iris overlaps the upper margin. On the left it is more nearly as in the younger stages, but wider (48μ). The free margin of the iris reaches now the enormous thickness of 56 to 80μ. The pigmented epithelium has rolled in more so that the elongated nuclei, free from pigment, are crowded together in the region of the ora serrata. The pupil is filled in part with pigment, evidently of choroidal origin. (Fig. 7.)

The right eye of the specimen 90 mm. long. The choroidal pigment has forced its way into the interior of the eye, and forms a conical-shaped mass like a plug in the iris, and extending into the depth of the vitreous cavity. Apparently on the external half of the iris the pigmented layer has become rolled in and folded upon itself in the interior of the eye, giving rise to a pigment mass over 100μ thick. No such mass is present in the left eye. The pigment on the inner or upper half of the iris is as in the younger stages.

The choroidal pigment entering the eye is in solid, vermiform strands.

THE RETINA.

The retina of *Typhlotriton* is much simpler than that of *Proteus*. In the latter all the layers typical of the perfect retina are still distinguishable (Kohl '92, p. 88). In the former the outer reticular layer has entirely disappeared, and the layers between the rods and cones and the inner reticular layer form a mass of cells that are homogeneous as far as ordinary histological methods permit one to determine. There are nowhere the slightest evidences of any rods or cones either in the largest or smallest individual. The nuclei of the outer nuclear, the horizontal and inner nuclear layers are alike. Müllerian fiber-nuclei have not been distinguished as such. This layer consists of about five series of nuclei, and measures 44μ in thickness in

the smallest (30 mm.), and 48μ in the largest (90 mm.) specimen; it is between 32 and 48μ in the specimen 70 mm. long.

The inner reticular layer is thin, but well defined. It is 6μ thick in the smallest specimen, 16μ in the specimen 70 mm. long. In section the ganglionic layer forms a U-shaped mass of cells. In the larger specimens it is about 60μ thick, and made up of from five to seven series of cells. The vitreous cavity is a widely flaring, trumpet-shaped structure, with its pointed end reaching about the center of the eye. In the older specimens it is filled by fibers and cellular tissue, apparently continuous with the choroid ingrowth from the pupil. (Fig. 8.)

The optic nerve is 17μ in diameter in the 30 mm. specimen. In the largest specimen it is 24μ thick without its sheaths. At its passage through the pigmented layer of the retina it is contracted to a width of but 14μ. Within this layer it expands to 28μ. After passing directly through the ganglionic layer it is distributed to the cells of this layer, some of the fibers being bent at an acute angle to reach the cells near the entrance of the nerve into this layer. A large number of isolated pigment granules are found associated with the nuclei of the optic nerve within the eye from its entrance to the ganglionic layer. (Fig. 6.) There is no sheath of pigment such as is found in *Typhlogobius*. Pigment cells are also occasionally present in the very center of the eye (Fig. 6), and are presumably associated with the optic nerve. The sheath of the optic nerve consists of a direct continuation of the choroid layer, which is for a shorter distance pigmented, and of a continuation of the sclera.

Blood-vessels do not enter the eye with the nerve, and none were with certainty detected, except in the largest individual, where they are closely associated with the choroidal mass of tissue that has grown into the eye through the pupil.

SUMMARY.

1. The eye lies just beneath the skin. The skin is but little thinner over the eye than elsewhere, and shows no structural characters different from those of neighboring regions.

2. The eye muscles have vanished.

3. The lens has vanished, and its place has in part become filled by an ingrowth of choroidal tissue containing pigment.

4. The vitreal body is very small, if present at all. The vitreal cavity is a funnel or trumpet-shaped space.

5. The pigmented layer of the retina is a pavement epithelium with indistinct cell boundaries, and with occasional pigmented processes extending into or through the nuclear layers.

6. Rods and cones are not formed.

7. The outer reticular layer has disappeared.

8. The inner and outer nuclear layers form one layer, cells indistinguishable from each other.

9. The inner reticular layer, as usually with degenerate eyes, is relatively well developed.

10. The ganglionic layer is well represented and connected with the brain by the well developed optic nerve.

11. The epithelial portion of the iris is at first simple, with an outer pigmented and an inner colorless layer. With age the margins of the iris become folded inward in such a way that the pigmented layer may be thrown into folds in the interior of the eye, while the colorless layer is but little affected.

12. Pigment granules, and rarely pigmented cells, are associated in the eye with the optic nerve.

13. The eye is more degenerate than that of the European *Proteus*. It is less degenerate than that of the North American blind fishes *Amblyopsis*, *Typhlichthys*, and *Troglichthys*, but much more so than that of the species of *Chologaster*.

PAPERS EXAMINED.

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KOHL, C., '92 and '93; Rudimentäre Wirbelthieraugen. Bibliotheca Zoologica. Heft 13 und 14.

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PLATE III.

DESCRIPTION OF FIGURES.

All figures except those from photographs have been drawn with the aid of the camera lucida.

1. Pigment epithelium.

3-7. Outer nulear to inner reticular layers of the normal retina.

8. Inner reticular layer.

9. Ganglionic layer.

chr. Choroid.

cps. Blood corpuscles.

i^1. Outer layer of the iris, epithelial.

i^2. Inner layer of the iris.

n. op. Optic uerve.

p. Pupillary margins.

scl. Sclera.

z. Pigment cells which have entered the eye.

Fig. 1. Outline sketch of part of the section of the head of a specimen 90 mm. long, showing the position of the eye.

Fig. 2. Right eye of a specimen 80 mm. long.

Fig. 3. Exit of the optic nerve of the same.

Fig. 4. Iris of the left eye of the same specimen.

Fig. 5. Upper half of iris of the right eye of a specimen 70 mm. long.

Fig. 6. Right eye of a specimen 70 mm. long.

Fig. 7. Right eye of a specimen 90 mm. long.

Fig. 8. Exit of optic nerve of the same eye.

Fig. 9. Lens of a specimen 72 mm. long.

PLATE III

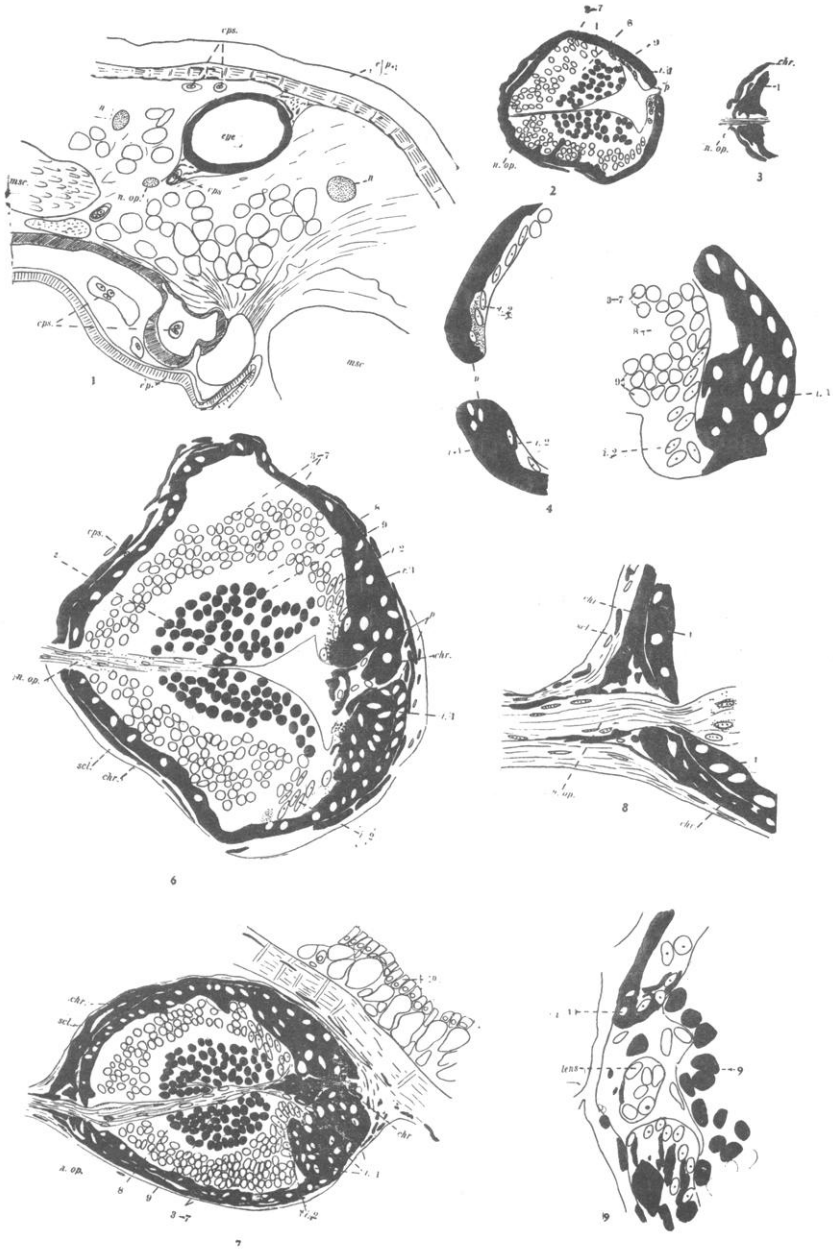

PLATE IV.

DESCRIPTION OF FIGURES.

Figs. 10-12. The heads of the three cave salamanders of North America. The heads were subjected to the same treatment to prepare them for photography, and the photographs were taken under approximately the same magnification.

Fig. 10. The head of a *Spelerpes maculicauda* 54 mm. long. × 14.

Fig. 11. The head of a *Typhlotriton spelæus* 54 mm. long. × 15.

Fig. 12. The head of a *Typhlomolge rathbuni* 47½ mm. long. × 14

PLATE IV

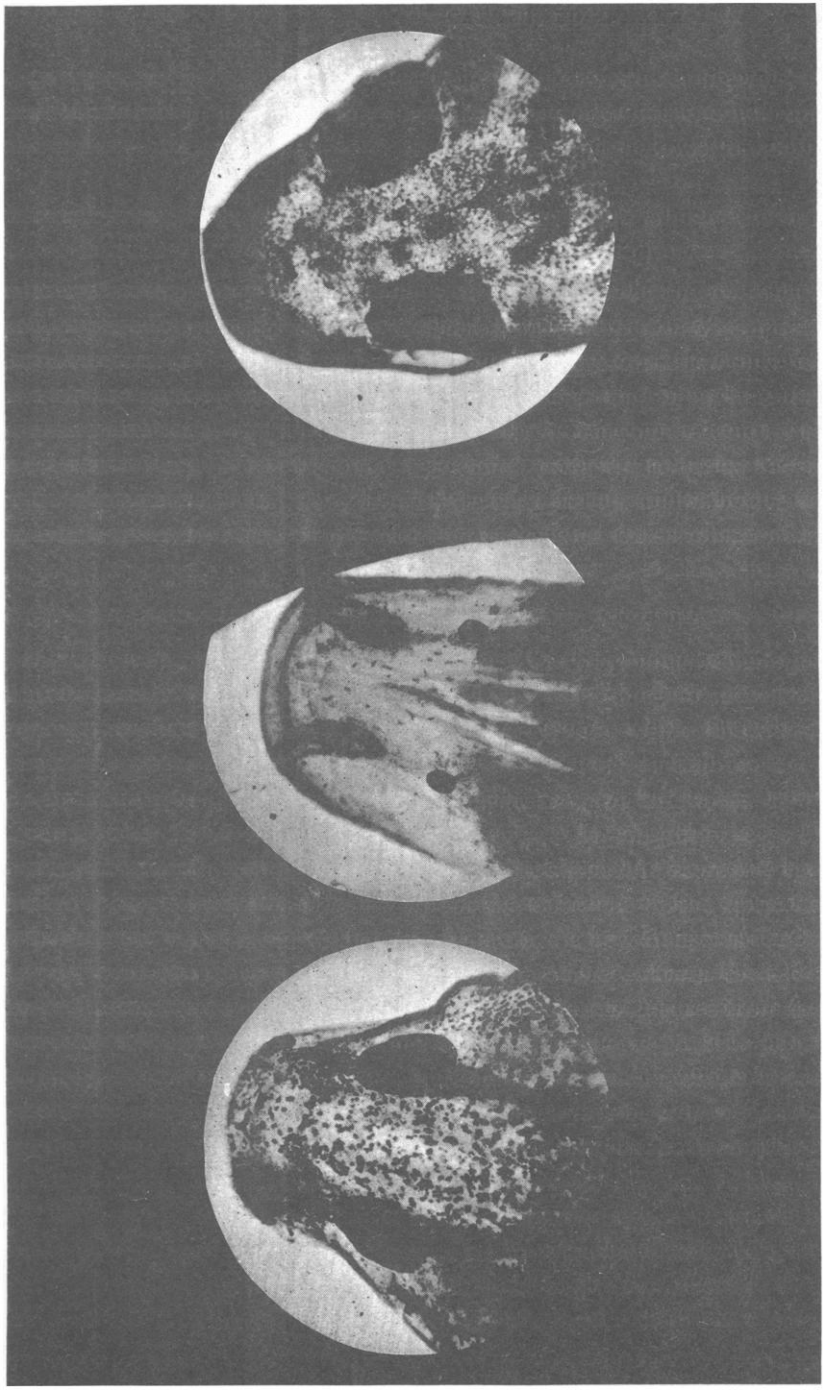

Figure 10 at top; 11 at bottom: 12 between.